GONDWANAN GRASSES IN THE AUSTRALIAN FLORA*

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Summary

All the currently recognized major groups of the Poaceae (the grass family) with the exception of the pooids, are postulated to have had a Gondwanan origin. There is no hard evidence for this belief, the fossil record of the family being extremely poor and giving little assistance in the study of the palaeogeography and evolution of taxa. The evolution of the major groups, and in some cases genera and species of grasses, is reviewed in relation to Gondwanic events, both generally and in relation to Australia, in the light of studies from biogeography, plate tectonics, numerical methods and cytogeography.

Introduction

Due to their economic importance the grass family has probably been researched more intensively, from many different angles, than any other plant family. Accurate distributional data are available from the many accounts of the family that exist for most regions of the world and from these data a number of biogeographical analyses at global or regional levels has been undertaken at various ranks. Examples are the papers of Hartley (1950, 1958a, 1958b, 1973) and Hartley and Slater (1960) for tribes and subfamilies; the chorological studies of Clayton (1975), Clayton and Cope (1980a, 1980b) and Cross (1980); the biogeographical work of Clifford and Simon (1981) and Simon (1981, 1986, 1988); and the distributional studies of Australian (Hattersley 1983; Prendergast & Hattersley 1985; Prendergast et al. 1986; Prendergast 1989) and southern African taxa (Ellis 1977; Ellis et al. 1980; Gibbs Russell 1986; Vogel et al. 1978) in connection with the distribution of taxa with reference to their decarboxylation types. Despite all this work however, knowledge pertaining to the origins and evolution of major groups (used here as more or less equivalent to subfamilies, see **Table 2**), genera and species of grasses remains in the realm of speculation mainly due to their very poor fossil record. Grasses are found in all regions of the world inhabited by plants and although all except the pooids are thought to have had a Gondwanan origin (Clayton 1981) (**Fig. 1**), this has been deduced by a study of their current biogeography in relation to their probable phylogeny rather than by their present day distribution being "Gondwanic" in the nature of that of the "southern" families Myrtaceae, Proteaceae and Restionaceae (Johnson & Briggs 1981). In addition to current distribution patterns of grasses we need to look to some other sources of evidence in attempting to target those major groups, genera and species we assume to be Gondwanan. Avenues open for investigation include **palaeobotany, tectonic history, numerical methods** and **cytogeography.**

Palaeobotany

The best fossil record is from the United States of America (Thomasson 1980, 1987) (**Table 1**) and even this is inadequate to help in understanding phylogeny. In Australia, older monosulcate pollen, characteristic of monocotyledons and a few dicotyledons, has been found from the early Aptian stage of the lower Cretaceous (125 m.y.B.P.) (Dettman 1981).

The first appearance of fossil grass pollen in Australia is in the early Eocene (54 m.y.B.P.) of the Tertiary period (Smith 1982), as is the case elsewhere in the world, but records become more common in the Pliocene (10 m.y.B.P.) (Martin 1981). None of

the pollen is identifiable to genus. There are also Tertiary leaf fragments that have been assigned to the genus *Phragmites* and form genera *Bambucites* and *Poacites* (see Duigan 1951) but these records date back to the last century when palaeontological methods were very crude (Thomasson 1980).

Tectonic History

It is necessary to place the few existing Australian grass fossils in the context of the timing of the origin of the angiosperms and of the tectonic history of the region in relation to the fragmentation of Gondwanaland. An excellent essay of these events and the impact they had on the evolution of the Australian flora is that of Barlow (1981), although ideas on Gondwanaland reconstruction have been altered recently by the inclusion of many more areas of Asia (Audley-Charles 1987). Details from these papers, together with other papers dealing more specifically with the grasses (Clayton 1975, 1981; Clifford & Simon 1981; Hattersley 1983; Simon 1986, 1988), can be used to develop a plausible account of how subfamilies, genera and species of Gondwanan grasses evolved and were distributed, with particular reference to Australia.

A discussion of the age of the grasses has to commence with discussion of the origin and age of the angiosperms in general. Because the features of double fertilization and triploid endosperm are unique to the angiosperms it is generally assumed that they are monophyletic although a few views have been put suggesting that they could be polyphyletic (see references in Barlow 1981). Evidence exists that angiosperms had a Gondwana-wide distribution before the fragmentation of the supercontinent. Monosulcate pollen (indicative of monocotyledons and dicot Annonales and Nymphaeales) and tricolpate pollen, characteristic of all other dicotyledons, is known at several widespread localities in the lower Cretaceous (see **Table 1**). There are two main areas where the angiosperms are postulated to have originated, one in western Gondwanaland, possibly tropical Africa (Raven & Axelrod 1974) and the other being a zone from India to Fiji (Smith 1963; Takhtajan 1969) in eastern Gondwanaland. Although the latter region had fallen from favour (Schuster 1976) the recent paper by Audley-Charles (1987) has offered new evidence for regarding this region more favourably.

The grass family appears to have existed almost as long as the angiosperms (**Table 1**), although they are thought to have come on the scene after the angiosperms were well diversified (Gould & Shaw 1983). The fossils listed in the table give little clue as to when the major groups and genera of grasses diverged from each other, and which areas of Gondwanaland could be regarded as their cradle. In this respect they are no different from other Angiosperm families for which schemes have been given for the radiation of contemporary taxa, e.g. Proteaceae (Johnson & Briggs 1975, 1981).

Clayton (1981) (**Fig. 1**) suggested the Flagellariaceae or a similar group as an evolutionary precursor to the grasses. This hypothesis has been tested by recent cladistic studies (Campbell & Kellogg 1987; Kellogg & Campbell 1987) where the Flagellariaceae and Joinvilleaceae have both been used as outgroups. While their preliminary results to date do not seem to indicate either family as particularly appropriate, there do not seem to be any realistic alternatives. Clayton's placing of the major groups, both their position in relation to each other, to Gondwanan and non-Gondwanan areas, and to the type of carbon decarboxylation, looks plausible. The arundinoid group, for example, stands as fairly central in the scheme and is postulated to be the core group from which all non-bambusoid groups arose. A similar pattern was proposed 25 years earlier by Stebbins (1956) in his familiar amoeboid cross section of an evolutionary tree in which the hypothetical ancestor, indicated by a star, is believed to be related to the Flagellariaceae, Restionaceae or primitive Liliaceae. A contrary view (Tsvelev 1969) is that pooids are ancestral and this is supported by recent cladistic work (Kellogg & Campbell 1987).

Although the major groups (subfamilies or tribal groupings) and tribes of grasses are distributed in the world in broad latitudinal belts (Hartley 1950; Cross 1980; Simon 1988) more or less correlated with their physiological adaptations to different climates, two-thirds of the genera are restricted to one continent (Clayton 1975). From this it is deduced that the major groups were established before the breakup of Gondwanaland and a large proportion of the genera became differentiated after this event. An extension of Clayton's biogeographic analysis of genera based on the floristic regions of Tahktajan

Table 1. Geological time scale since the Jurassic, with accompanying tectonic activity, known grass fossils and major developments affecting grass evolution.

Age	Period	Epoch	Tectonic event	Grass fossils	Life
2.5	QUAT	Pleistocene		12 records (Afr, U.S.)	Widespread glaciation
10	T	Pliocene		5 records (N&S Am, Eu)	
	E	Miocene	N.Am = S.Am Aust = Asia Afr = Eurasia	Many grass fossils (Europe, U.S.A.)	
20	R				
30					
	T	Oligocene	S.Am|Ant|Aust (end of temp. link)	10 grass fossils (Colorado, Montana)	Evolution of grazing animals
	I				
40					
	A	Eocene	India=Asia	?*Poacites* (Argentina)	Most angiosperm families exist
				?*Bambusites*, ?*Poacites*	
50	R			?*Phragmites* (Australia)	
				Fossil grass pollen in Australia	
	Y				
60		Palaeocene			
	U		Eurasia|Afr		Numerous modern angiosperm families and genera
	P				
	P		N.Z|Aust|NCal		
70	E			?*Phragmites* (Texas)	
	R			?*Graminopyllum* (Mongolia)	
	C			?*Arundo* (Nebraska)	
80	R				
	E				
	T				
90	A		Afr|S.Am (WG)		
	C				
	E				
	O				
100	U		India|Mad|Afr		
	S		WG|EG		
110					
	C			Trisulcate pollen (Australia)	Angiosperms widespread
	R				
120	L E				
	O T			Monosulcate pollen (Australia)	Angiosperms in Australia
	W A				
	E C				
130	R E				Angiosperms in N Gond & S Laurasia
	O				
	U				
	S				
140			Gondwanaland		
		JURAS			

Data on grass fossils are summarised from Diugan (1951) and Thomasson (1987). A question mark preceeding the generic name indicates the identification of the fossil is not unequivocal.

(1969) (Simon 1986), using a number of classificatory programs of the numerical taxonomy package (NTP) of Belbin *et al.*(1984), shows the genera of tropical Australia to be more closely related to those of tropical Asia than to those of other regions of Australia (**Figs 2–4**). At species level the relationship to tropical Asia is still fairly significant (Simon 1988). In the light of the most recent theory concerning the structure of Gondwanaland since pre-Jurassic times (Audley-Charles 1987) (**Fig. 5**), the Asian connection makes

more sense in terms of the time available to establish biogeographic links than the alternative theories that hypothesise that the first contact between Australia and a large proportion of Asia was during the mid-Miocene.

Because the evidence supports development of at least the sub-familes prior to separation of the elements of Gondwanaland we need to consider the major groups separately rather than look at the grasses as a whole. The best way is to look at each major group in turn and postulate on how they could have spread throughout Gond-wanaland, including the plate of east Gondwanaland that incorporates Australia. We can then look at present-day climatic and edaphic conditions within Australia to interpret how diversification of genera and species may have taken place in more recent times.

Clayton's figure (**Fig. 1**) on the phylogeny of the grasses has no associated time framework and is based on the assumptions of what are primitive and advanced characters in extant members of the family. Primitive and advanced characters based on floral morphology were first listed 40 years ago by Hubbard (1948). To these may be added the now well-known cryptic characters derived from anatomy, cytology and physiology that have all had a great impact on the classification since the 1930's (Avdulov 1931; Stebbins 1956 and other references in Clayton & Renvoize 1986). These cryptic characters are now more important in the classification of subfamilies and major groups than those based on floral morphology and were considered in some depth at the 1986 Symposium on Grass Systematics and Evolution at the Smithsonian Institution (Soderstrom *et al.* 1987).
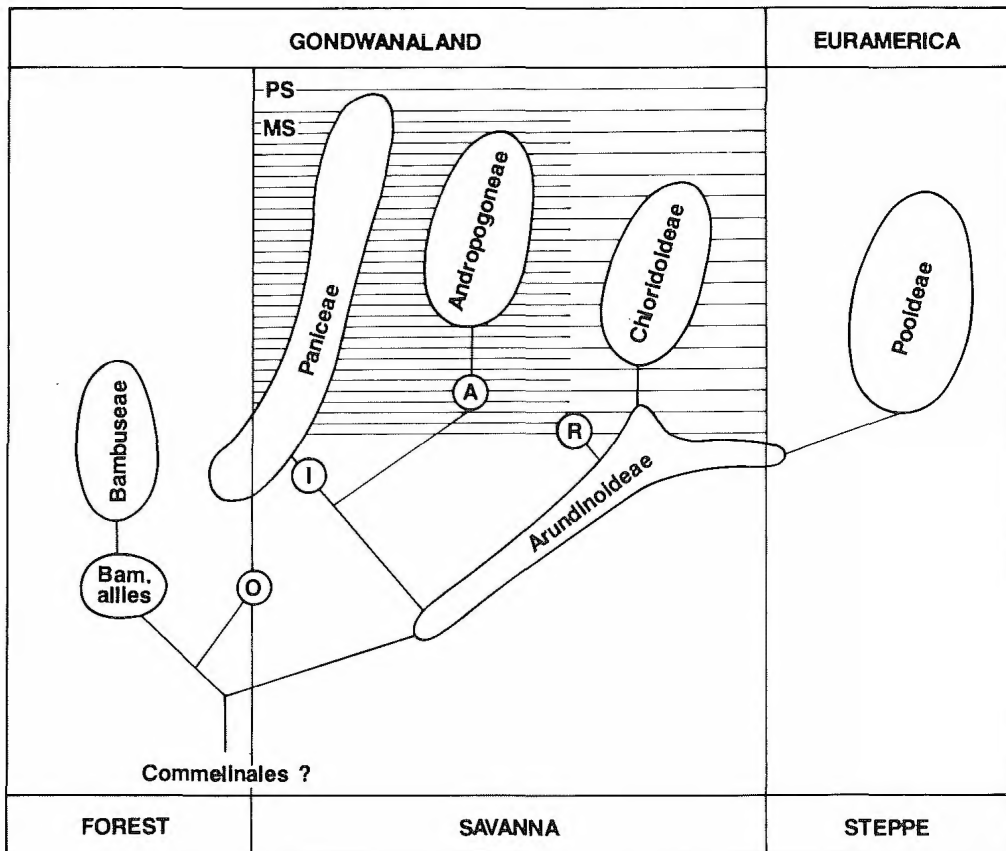
Fig. 1. Suggested relationships among the major groups of grasses. A = Arundinelleae. I = Isachneae. O = Orzeae. R = Aristideae. C_4 metaboloism is indicated by horizontal lines: it is divided into the MS and PS types of Brown (1977). (From Clayton, 1981; redrawn by permission from *Annals of the Missouri Botanical Garden* 69: 6).
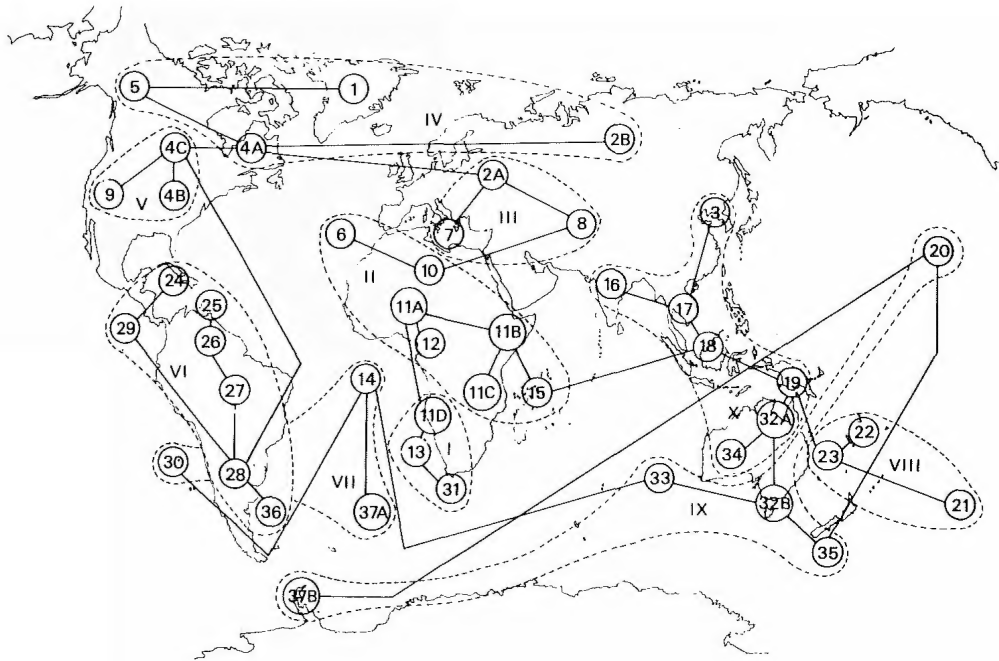
Fig. 2. Minimum spanning tree of world floristic regions based on distribution of grass genera.
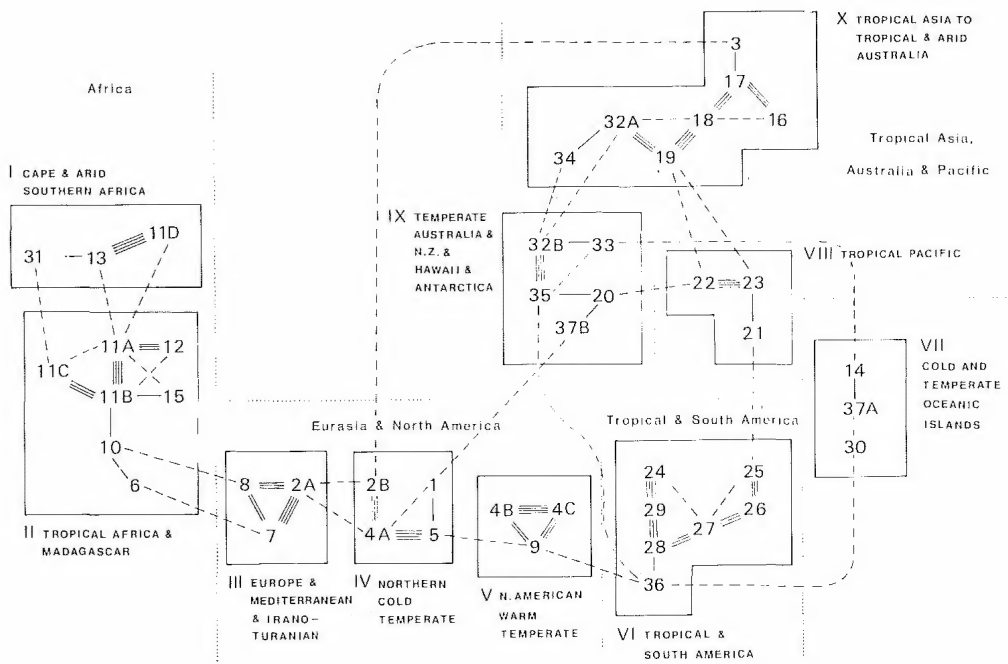
Fig. 3. Two neighbour network of world floristic regions based on distribution of grass genera. Floristic regions as in Fig. 2.
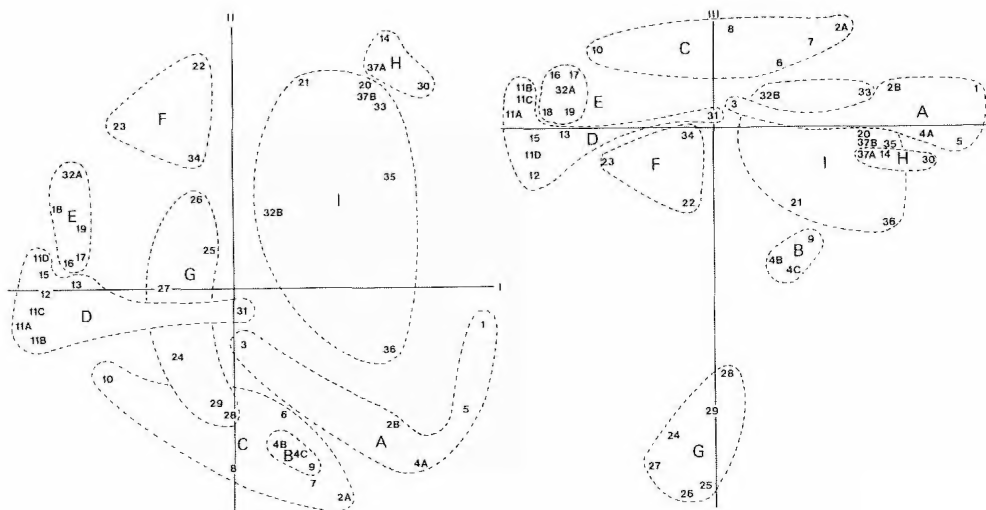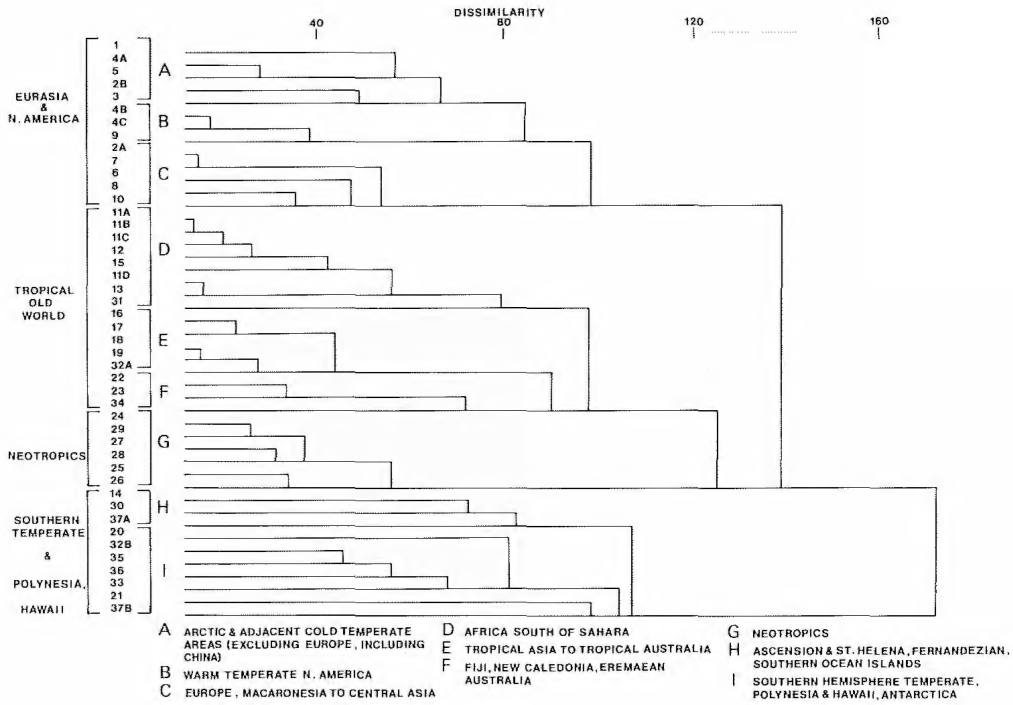
Fig. 4. Dendrogram and principal co-ordinates of world floristic regions based on distribution of grass genera. Floristic regions as in Fig. 2.

Numerical Methods

Over recent years, with the increase in the use of computers in attempting to solve problems of classification and evolution of plant groups, numerous numeric methods have been applied to the grasses. The data that exists for the family are greater than that for any other family, the most recent data base for genera being that of Watson & Dallwitz (1988). A good recent summary of numerical methods is that of Baum (1987) whereas the papers of Kellogg and Campbell (Campbell & Kellogg 1987; Kellogg & Campbell 1987) give the current state with regard to cladistic studies in the family. For example the arundinoids, as presently constituted, appear to be polyphyletic (Kellogg & Campbell 1987), with all other subfamilies being monophyletic and interspersed among them.

The arundinoids are thus not a natural group and should not be treated as such when regarded as a "group" from which other groups arose. Within the major groups some contemporary genera are suspected of being polyphyletic e.g. *Eragrostis* and allies (Jacobs 1987) and may have to be reclassified.

Cytogeography

Cytological data of value for illustrating cytogeographic pathways of Australian grass taxa is available for only three taxa – *Themeda triandra* (as *T. australis*) (Hayman 1960), *Danthonia* (Brock & Brown 1961) and the tribe Neurachneae (Prendergast & Hattersley 1985). Accordingly the use of karyology as an aid in interpreting the evolution of groups of Gondwanan grasses in Australia offers little assistance.
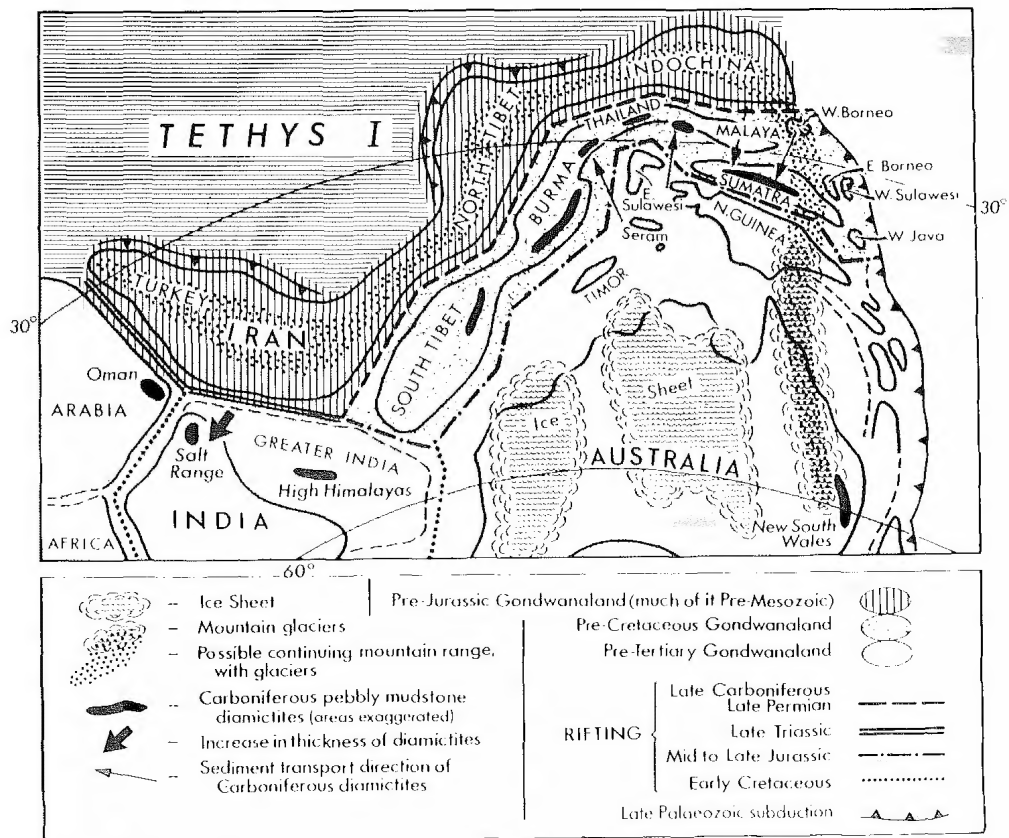

Fig. 5. Reconstruction of eastern Gondwanaland since pre-Jurassic times. (From Audley-Charles, 1987; reprinted by permission from the author and Clarendon Press).

Hybridization, polyploidy and aneuploidy have been the active features in the chromosomal evolution of the grasses (de Wet 1987). Two theories have been put forward to explain the evolution of the major groups: one theory (Clayton 1981) has the arundinoids (x = 6,7,9,10,11 or multiples of these) giving rise to the pooids (x = 7), the chloridoids (x = 9,10) and subfamily Panicoideae (x = 9,10) with the bambusoids (x = 11,12) being derived from pre-arundinoids; the second theory proposes an independent origin of all groups from an original complex with (x = 5,6,7) (Hubbard 1948; Stebbins 1985).

Polyploidy has occurred in both *Themeda triandra* and *Danthonia* species in their adapting to the more arid regions of the continent whereas in the Neurachneae the only diploid species is restricted to the Macdonnell Ranges and is interpreted as indicating a relictual presence there (Prendergast & Hattersley 1985).

Evolution of major groups of grasses in relation to Gondwanic events

Table 2 lists all the Australian genera in subfamilies or major taxonomic groups with a breakdown to the floristic elements recognized by Clifford and Simon (1981), and the number of species, both in Australia and the World. It is an expansion of **Table 2** of Clifford and Simon (1981). The percentage frequencies of genera in each major group of grasses in each of the world floristic regions of Takhtajan (1969) are given in **Maps 1–6** where the data are from Simon (1986). The numbers of species of major groups for regions of the Old World have been shown in the maps of Cross (1980).

1. Andropogonoids

The Indian and Indo-Chinese regions have the highest representation of both genera (**Map 1**) and species (Cross 1980). In general the Old World has many more genera and species than the New World, where only in one region (the Caribbean) are there more than 20% of the total number of andropogonoid genera. Furthermore no region has more than 20% of their grass floras with andropogonoid species (Hartley 1958a). Areas with a distinctly seasonal (monsoonal) rainfall of 700–1500 mm on well-drained soils have the highest representation of andropogonoids as shown in **Fig. 6**. These are the core savanna communities of Johnson and Tothill (1981). The andropogonoids could have arisen via the Arundinelleae (Clayton & Renvoize 1986), which is placed with the panicoids by some authors because it shares characters of dimorphic florets and a geniculate awn. The Arundinelleae shows a dichotomy between the arundinelloid (*Arundinella* and *Jansenella*) and loudetioid lines (all other genera) and it is probably among the loudetioid genera that we must look for the out-group of the andropogonoids. The extant loudetioid members have their main distribution in the Old World tropics with the exception of Australia (Phipps 1967). All the loudetioid genera are in tropical Africa and it is to this part of western Gondwanaland that we must look as the possible cradle of the andropogonoids. From here the group could have spread to northern Gondwanaland (the Indian plate) before the breakup of the super-continent in the mid-Cretaceous and then through other parts of tropical Asia and Australia. This dispersal could have occurred either from the Eocene, when the Indian plate collided with Eurasia, and into Australia after collision of the latter with Sundaland in the mid-Miocene (Powell *et al.* 1981) or much earlier if a recent theory concerning the composition of Gondwanaland (Audley-Charles 1987) is correct. There is almost an equal number of Australian andropogonoid genera belonging to Clifford and Simon's Gondwanan, Old World Tropics and Indo-Malayan elements (**Table 2**). They are all really Gondwanan in terms of their origin, with the two latter elements not occurring on the American plate of west Gondwanaland. There is only one genus (*Spathia*) of the Endemic element and its one species probably evolved fairly recently from *Dichanthium*. The average numbers of species/genus in these two latter elements is usually fairly small, although the genera *Iseilema* and *Thaumastochloa* have speciated fairly prolifically. At species level there are some anomalous Gondwanic distribution patterns that require explanation(s) other than plate tectonics if the thesis of species being of comparatively recent origin is correct. Examples are *Heteropogon contortus*, native to all pantropic areas and *Eulalia aurea*, *Hyparrhenia filipendula* and *Themeda triandra* (if *T. australis* is not regarded as distinct), native to all parts of the Old World tropics. Although explanations have been given for Miocene and Pliocene connections at species level in the Old World (Moreau 1952; Schnell 1962) there is a possibility of the distribution being due to
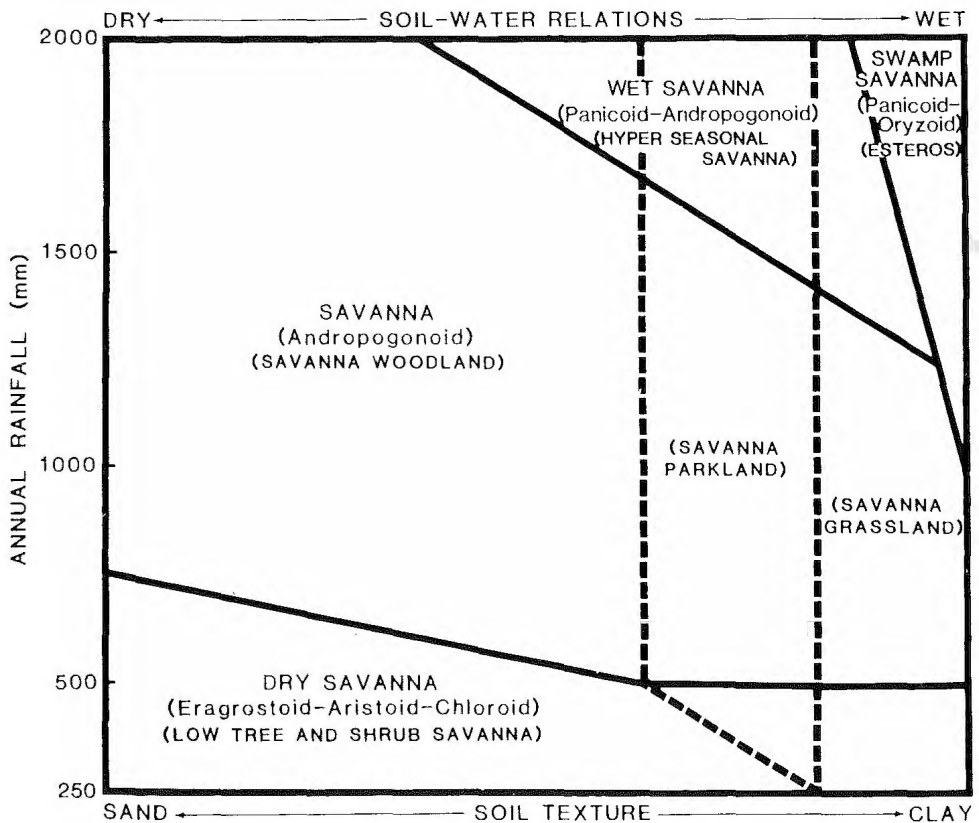
Fig. 6. Classification of savannas of the world. (From Johnson & Tothill 1986; reprinted by permission from Australian Academy of Science).

commercial exchanges at least between eastern Africa and Malesia for nearly 1000 years (Clayton 1969). The pan-Atlantic connection of species is more problematic (Schnell 1961). The biogeography of the series of *Cymbopogon* (Soenarko 1977) can be accounted for more rationally by the tectonic theory with all five series being contiguous or nearly so in their distribution patterns, with the exception of the series *Citrati*. Species of *Citrati* could have spread between Africa and Indo-China (Schnell 1962) or along arid corridors in the manner illustrated by van Steenis (1979).

The paucity of andropogonoid representation in the New World could be explained by two contrasting but not mutually exclusive hypotheses. It may either be an indication of a late arrival there in their evolutionary development or else there were few ecological niches available to spread into.

2. Panicoids

The south tropical African floristic region is best represented at both generic (**Map 2**) and species level (Cross 1980), although the latter paper only gives figures for the Old World. Other regions with a high number of panicoid genera are located in the Americas, Africa and Australia. The panicoids are best developed in the wet savannas with an annual rainfall of more than 1500 mm on moisture-retaining soils (**Fig. 6**) (Johnson & Tothill 1981). Panicoids have a variety of photosynthetic pathways (C_3 and C_4 of both Kranz MS and PS types) enabling different species to exploit wet, high-light, shaded and arid habitats. From an east African-Madagascan origin in west Gondwanaland of the subfamily Panicoideae (to which the panicoids and andropogonoids both belong) the panicoids are thought to have spread early throughout Gondwanaland. If the arundinelloid line of the Arundinelleae is regarded as the ancestor for the panicoids this would be a

plausible theory as the genus *Arundinella* is pan-Gondwanic in its distribution. The Australian panicoids have a higher endemic component than the andropogonoids. For example there are 13 genera of the Endemic element and of the other floristic elements a high percentage of the species are endemic (**Table 2**). These endemic species are probably of recent rather than ancient origin and evolved by adapting to environmental changes on the subcontinent in the Tertiary, even though the genera themselves originated before continental rafting.

3. Chloridoids

As with the panicoids the chloridoids have most genera in the south tropical African floristic region (**Map 3**) as they do at species level in the Old World (Cross 1980). They are best developed in areas with an annual rainfall of less than 700 mm falling mainly in summer (**Fig. 6**) i.e. the dry savannas (Johnson & Tothill 1981), although there are more species in the wetter tropical regions of Africa, Asia and Australia than in the arid zones. The percentage method (Hartley & Slater 1960) indicate regions of high chloridoid presence in the arid belts centred on the tropics of Cancer and Capricorn. Whereas the total number of grass species is not large, a very high proportion of those species that have been able to adapt, are chloridoids. The percentage method may only be indicating areas of relative specialisation rather than areas of origin. Treating such areas as places of relative specialisation is in line with Smith-White's (1982) conclusion that spread and speciation in the arid areas of Australia is based on the species growing on the periphery of those areas. Another reason for Hartley and Slater's high figures for the arid region is that they included *Aristida* in the chloridoids whereas subsequent work has shown this genus better placed with the arundinoids. When looking only at Australian chloridoid genera they show a similarity to the panicoids in terms of their breakdown into the floristic elements of Clifford and Simon (Endemic:Old World Tropics:Gondwanan – 12:9:9 chloridoid compared to 13:7:15 panicoid). As with the panicoids endemic genera and species probably arose relatively recently in response to local conditions. For example Jacobs (1982, 1987) postulates a diversification at and below the species level within the endemic genera *Triodia* and *Plectrachne* in the late Pleistocene, with *Triodia* (and the recently described genus *Symplectrodia*) adapting to monsoonal and arid regions of central, northern and western Australia and *Plectrachne* to the Mediterranean climate of southwest Western Australia. The African plate is suggested as an area for the origin of the chloridoids (Hartley & Slater 1960) on the basis that, of the genera occurring on more than one continent, all except one are found in Africa. However Jacobs (1982, 1987) does not postulate more than that the chloridoids originated in Gondwanaland. In terms of their phylogeny it appears that the group may be polyphyletic (Jacobs 1987) as may also be some of the larger genera e.g. *Eragrostis* and *Sporobolus*.

4. Bambusoids

In this treatment the bambusoids are regarded in the broad sense to include the woody bamboos, the herbaceous bamboos, the oryzoids and the centothecoids. The woody bamboos are unique in terms of the biogeographic range their genera occupy, from tropical lowlands to montane zones more than 4000 m high and latitudes from 46°N to 47°S (Ohrnberger & Goerrings 1985; Soderstrom & Calderon 1979). Floristic regions with high representation of bambusoid genera are shown in **Map 4**. Australia is poorly represented with supposedly one genus (*Bambusa*) consisting of three species. In reality the Australian species probably represent three distinct genera from two different tribes though further work is required to clarify the situation. The herbaceous bamboos (tribes Olyreae and Phareae) are not found above 1500 m and are centred in the neotropics; only two genera (*Leptaspis* and *Scrotochloa*) occur in Australia. The oryzoids (rice grasses) are pantropic, associated with wet habitats (**Fig. 6**), the swamp savannas of Johnson and Tothill (1981); they are bamboo allies, possessing at least six of the ten anatomical characters that demarcate the bambusoid core group i.e. the woody and herbaceous bamboos (Soderstrom & Ellis 1987). The tribes Centotheceae and Ehrharteae are treated as bambusoids in this paper although not regarded as such by Soderstrom and Ellis (1987). The first is a pantropic group of rainforest-floor species and the second is represented in warm temperate to montane areas of the Old World. The regions with most bambusoid genera are Indo-China, the Caribbean, Eastern Asia, the Central Brazilian and Amazon regions of tropical America, and India. The bambusoid genera have a much

Table 2. Biogeographic elements (updated and expanded from Clifford & Simon 1981) of Australian grass genera.

Biogeographic Elements	Total	Genus	Species Number Australia	Total
1. Andropogonoid				
Endemic	1	*Spathia*	1	1
Australasian	0	–		
Indo-Malayan	11	*Apluda*	1	1
		Chionachne	2	7
		Coix	2	5
		Dimeria	3	35–40
		Eremochloa	3	9
		Germainia	3	9
		Iseilema	14	c.20
		Pogonatherum	1	3
		Polytrias 1	1	1
		Pseudopogonatherum 2	2	
		Thaumastochloa	8	8
Old World Tropics	13	*Arthraxon*	2	c.10
		Capillipedium 2	c.14	
		Cymbopogon	9	c.40
		Dichanthium	6	c.20
		Eulalia	4	c.30
		Hyparrhenia	1	55
		Microstegium	1	c.15
		Ophiuros	1	4
		Rottboellia	1	?1
		Saccharum	1	35–40
		Sehima	1	5
		Themeda	3	18
		Vetiveria	4	10
Africa	0	–		
America	0	–		
Gondwanan	11	*Bothriochloa*	7	c.35
		Chrysopogon	6	26
		Elionurus	1	15
		Hemarthria	1	12
		Heteropogon	2	6
		Imperata	1	8
		Ischaemum	7	c.65
		Mnesithea	5	32
		Schizachyrium	7	c.60
		Sorghum	14	c.20
2.2. Panicoid				
Endemic	13	*Arthragrostis*	2	2
		Calyptochloa	1	1
		Chamaeraphis	1	1
		Homopholis	2	2
		Hygrochloa	2	2
		Neurachne	6	6
		Paractaenum	1	1
		Paraneurachne	1	1
		Plagiosetum	1	1
		Thyridolepis	3	3
		Uranthoecium	1	1
		Whiteochloa	5	5
		Zygochloa	1	1
Australasia	1	*Cleistochloa*	3	3

Indo-Malayan	6	*Ancistrachne*	2	3
		Garnotia	1	29
		Pseudoraphis	3	6
		Spinifex	4	4
		Xerochloa	3	3
		Yakirra	6	7
Old World Tropics	7	*Alloteropsis*	2	5
		Coelachne	1	10
		Cyrtococcum	1	11
		Holcolemma	1	4
		Ottochloa	2	4
		Thuarea	1	2
Africa		*Entolasia*	3	5
America	0	–		
Gondwanan	15	*Arundinella*	4	c.50
		Brachiaria	18	c.100
		Cenchrus	3	22
		Digitaria	32	c.230
		Echinochloa	9	30–40
		Eriochloa	6	30
		Isachne	3	c.100
		Oplismenus	5	5
		Panicum	24	c.500
		Paspalidium	22	c.40
		Paspalum	3	c.330
		Pennisetum	3	c.80
		Sacciolepis	2	30
		Setaria	7	c.100
		Stenotaphrum	1	7
Ind-Mal/Tr.Am.	2	*Hymenachne*	1	5
		Ichnanthus	1	33

3. Chloridoid

Endemic	12	*Astrebla*	4	4
		Austrochloris	1	1
		Cynochloris	2	2
		Heterachne	3	3
		Monodia	1	1
		Oxychloris	1	1
		Planichloa	1	1
		Plectrachne	16	16
		Psammagrostis	1	1
		Symplectrodia	2	2
		Thellungia	1	1
		Triodia	c.35	c.35
Australasia	1	*Ectrosia*	11	11
Old World Tropics	10	*Brachyachne*	5	9
		Cynodon	2	c.8
		Dactyloctenium	1	13
		Elytrophorus	1	2
		Enteropogon	6	17
		Eragrostiella	1	5
		Lepturus	4	c.8
		Perotis	2	c.10
		Zoysia	2	c.10
Africa	1	*Triraphis*	1	7
America	0	–		
Gondwanan	9	*Chloris*	6	c.55
		Diplachne	2	
		Enneapogon	18	28
		Eragrostis	51	c.350
		Leptochloa	7	

		Microchloa	1	c.6
		Sporobolus	17	c.160
		Tragus	2	7
		Tripogon	1	c.30
Tmp N&S Am.	1	*Distichlis*	1	c.5

4. Arundinoid

Endemic	9	*Amphipogon*	5	5
		Anisopogon	1	1
		Cyperochloa	1	1
		Diplopogon	1	1
		Micraira	13	13
		Monachather	1	1
		Notochloe	1	1
		Plinthanthesis	3	3
		Spartochloa	1	1
Australasia	3	*Chionochloa*	1	c.20
		Erythranthera	2	
		Pheidochloa	1	2
Old World Tropics	1	*Elytrophorus*	1	2
Africa	1	*Triraphis*	1	7
Indo-Malayan	1	*Eriachne*	43	43
Gondwanan	1	*Aristida*	54	c.250
Cosmopolitan	2	*Danthonia*	3	1
		Phragmites	2	3–4

5. Stipoid

Cosmopolitan	1	*Stipa*	62	c.300

6. Pooid

Endemic	4(7)	*Australopyrum*	3	3
		Austrofestuca	2	2
		Dryopoa	1	1
		(Neuropoa)	1	1
		Pentapogon	1	1
		(Festucella)	1	1
		(Hookerochloa)	1	1
Australasia	2	*Dichelachne*	7	7
		Echinopogon	7	7
I-M,NZ,SAm	1	*Deyeuxia*	35	
SAm,NZ	1	*Amphibromus*	10	
Cosmopolitan	9	*Agrostis*	17	c.220
		Deschampsia	2	c.40
		Festuca	7	c.450
		Glyceria	3	c.40
		Hierochloe	4	c.30
		Poa	34	c.500
		Polypogon	2	18
		Puccinellia	2	c.80
		Trisetum	1	c.70

7. Bambusoid

Endemic	2	*Potamophila*	1	1
		Tetrarrhena	4	4
Indo-Malayan	3	*Lophatherum*	1	2
		Microlaena	2	
		Scrotochloa	2	2
Old World Tropics	2	*Centotheca*	2	4
		Leptaspis	1	5
America	1	*Bambusa*	3	c.120
Gondwanan	2	*Leersia*	1	18
		Oryza	3	c.20

higher degree of endemism than other major groups, with only two genera (*Leersia* and *Oryza*) being present in all four continents of America, Africa, Asia and Australia; species of both genera inhabit wet areas and are likely to have been spread by waterbirds. The cradle of the bamboos is open to much speculation. Some authorities think bamboos have been in existence for 100 to 200 million years (Breedlove in Farrelly 1984). If this is so they were well established in Gondwanic times but their subsequent development in the two main areas of the neo-tropics and tropical Asia must have been since the Eocene with the Indian or Australian rafts transporting the gene pool to the Asian region where they subsequently differentiated. There is a large variation in herbaceous genera in the neo-tropics. If herbaceous bamboos are considered primitive, or at least a large number of their character states are considered primitive, then the neotropics could be considered as a centre of origin for the group. Some of the herbaceous species also exhibit highly derived characters such as subterranean flowering.

The paucity of extant records in both Africa and Australia could be a result of extinction in these continents during phases of aridity (Moreau 1952; Galloway & Kemp 1981). The woody bamboos (tribe Bambuseae) are represented in Australia and Africa by one (two?) and three subtribes (one (three?) and 11 genera) respectively, whereas there are five subtribes present in both Asia and America (60 and 20 genera) (Soderstrom & Ellis 1987; Ohrnberger & Goerrings 1985).

5. Arundinoids

This group is so fraught with problems in its taxonomy that any attempt to understand aspects of phylogeny or origin of the group, either wholly or partially, must take this into account. A good overview of the subfamily is given by Renvoize (1981), who implied the group is made up of genera that cannot reasonably be accommodated in the other generally recognized subfamilies. Views differ as to component tribes of the group, with some tribes sometimes being placed with the bambusoids or chloridoids. Even the central tribe Arundineae has been treated differently in recent times, either being regarded as three tribes Arundineae, Danthonieae and Cortaderieae (Conert 1987) or as one (Renvoize 1981; Watson & Dallwitz 1988). One major problem is that there is no really satisfactory taxonomic treatment of *Danthonia*. Generic segregates have been made in an unbalanced manner on the basis of rather minor characters. Conert has erected generic segregates in Africa (Conert 1966, 1970, 1971) but resisted from doing so in Australasia, although he did recognize *Chionochloa*, segregated from *Danthonia* (Conert 1975). The genus *Rytidosperma* (*Notodanthonia*) has been segregated in Australasia and South America (Blake 1972; Connor & Edgar 1979; Clayton & Renvoize 1986; Nicora 1973; Tomlinson 1985; Zotov 1963) but as the character states do not correlate with the circumscriptions, we consider this separation to be premature pending the availability of more data. With the arundinoids being limited to the tribes listed by Renvoize (excluding Ehrharteae and Centotheceae) most arundinoid genera (**Map 5**) and species (Cross 1980) occur in the Cape and Namib regions of Southern Africa. Australia rates well at species level, with high numbers in all States, with *Danthonia* having many species in temperate areas and *Eriachne* and *Aristida* well represented in tropical areas. There are only six genera in the whole of the New World. As the arundinoids are classified at present they are polyphyletic (Kellogg & Campbell 1987) so hypothesising on their origin has little meaning. However, the Gondwanic nature of most of the genera is evident by their present distribution which is deduced to be the result of a long and independent evolution. The theory that the non-bambusoid groups arose from the arundinoids implies the latter have been pushed to the southern extremities and mountains of Gondwanic fragments by the groups they gave rise to (Clayton & Renvoize 1986). Although this appears to be the situation in a number of small genera, in other arundinoid genera evolution has continued, giving rise to genera with many species in different environments e.g. *Aristida* and *Eriachne* in arid regions, and *Danthonia* in Mediterranean climates. The arundinoids have adapted to more habitats than any other group and this is perhaps another indication of their relative age.

6. Stipoids

The stipoids are taxonomically treated as a single tribe Stipeae but opinions differ as to which subfamily they belong. Although traditionally placed with the pooids (see references in Barkworth & Everett 1987) increasing evidence is being assembled that
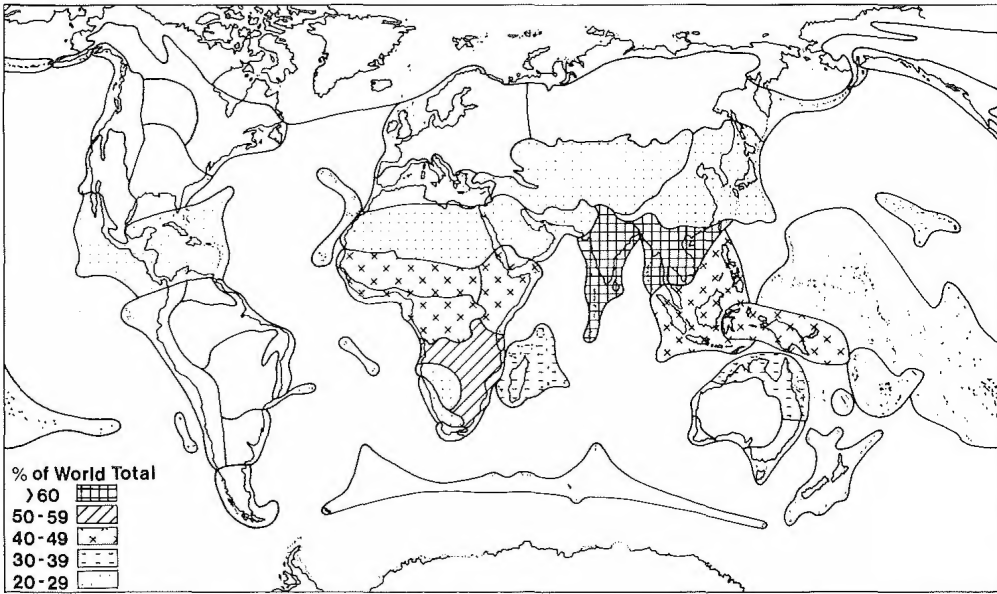
Map 1. Distribution of andropogonoid genera.

% of World Total
- >60
- 50-59
- 40-49
- 30-39
- 20-29
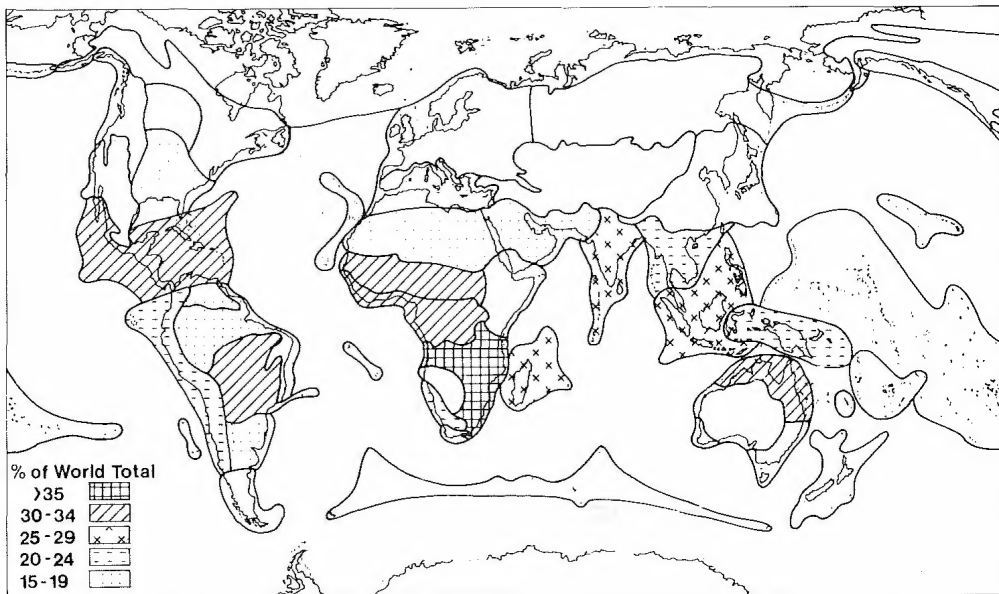
Map 2. Distribution of panicoid genera.

% of World Total
- >35
- 30-34
- 25-29
- 20-24
- 15-19

they do not really belong here (Campbell 1985; Macfarlane 1987). A current trend is to either place them with the arundinoids (Watson & Dallwitz 1988) or the bambusoids (references in Campbell 1985). Because of the uncertainty of their relationships it is probably best to regard them as a group in their own right when discussing their phylogeny. Within the group 10–15 genera have been described, being mainly variations from the first described and largest genus *Stipa*. However, as presently constituted, the genera are not natural and a recent attempt has been made to divide the group into monophyletic taxa without formal names (Barkworth & Everett 1987). There are five Australian groups of *Stipa* and the closest outgroup for the Australian species are those from Eurasia (especially *Achnatherum*). They believe the group to be Gondwanic in origin and that lines have radiated into Australia, Eurasia and America. Their "*Archeostipa*" could be interpreted as radiating from Antarctica into South America and Australia about 35 million years ago or even substantially earlier in the Oligocene when these parts of Gondwanaland were separating. The entry of stipoid grasses into North America was able to take place at the end of the Miocene 10 million years ago with the joining of the Americas. Some of the best known grass fossil remains are of antheocia of stipoid grasses from the Miocene and Oligocene deposits in the United States of America (Thomassen 1987) at a time when horses and pronghorn antelopes were evolving contemporaneously (Stebbins 1981). It is also possible that their spread into North America was from the north or from both directions. The derivation of the Eurasian lines is more problematical due the paucity of records in Africa (a few species of *Stipa*) and Asia (species of *Oryzopsis*, *Stipa* and *Trikeraia* all in the Himalayas). Ancestral *Stipa* may have been present in areas near the northern leading edge of the fragments of eastern Gondwanaland or in India.

7. Pooids

This is one of the largest subfamilies of grasses with 20% and 30% of the generic and species totals for the family (Macfarlane 1987). Its members predominate in regions of high latitude and altitude i.e. the temperate regions of the world. The centres of generic (**Map 6**) and species richness (Cross 1980) are Europe, the Mediterranean and the Irano-Turanian regions with gradually decreasing numbers for other less temperate regions. However pooids occur in most areas of the Northern and Southern Hemispheres in both Old and New Worlds where there is a suitable climate. How or when they achieved their present distribution is as much a mystery as to how they evolved. One view is that they spread to their present range relatively recently (since the Miocene) by traversing tropical regions along montane stepping stones. Entry from North to South America must have occurred on a small scale before the joining of these continents in the Pliocene but the rate of spread must have been accelerated subsequently. The entry to Australia of the relatively high pooid component of the grass flora, both the time of arrival and route of entry, is not established (Connor & Edgar 1986) but theories have been given (Clifford & Simon 1981). An entry route via Antarctica since the early Miocene seems feasible before the completion of the polar ice-cap formation whereas entry from the north (van Steenis in Burbidge 1960) appears less likely due to the great distances between blocks of elevated land. Audley-Charles (1987) does, however, postulate the formation and subsequent loss of islands that could have been used as "stepping stones". The pooids have been thought to have evolved from a section of C_3 arundinoids (Clayton 1981; Renvoize 1981) although recent cladistic studies (Kellogg & Campbell 1987) places the pooids at the base of the tree next to the outgroup *Joinvillea*. Such a relationship supports the hypothesis of Tsvelev (1969) that the grasses evolved from pooid type ancestors in high mountains with later movement to the plains.

Current Distribution of Australian Grasses

The present distribution of the grasses is a reflection of their pre-historic biogeography and their development and specialisation into a variety of habitats. One suite of environmental specialisations relates to their photosynthetic pathways and the pattern described for southern Africa by Gibbs Russell (1986) for the five subfamilies recognized by her can be applied generally as well as for Australia.

"Panicoideae (mainly C_4 malate formers) in mesic summer rainfall regions; Chloridoideae (mainly C_4 aspartate formers) in arid summer rainfall regions; and Arundinoideae (mainly C_3) in regions with more than 40% winter rainfall. Pooideae
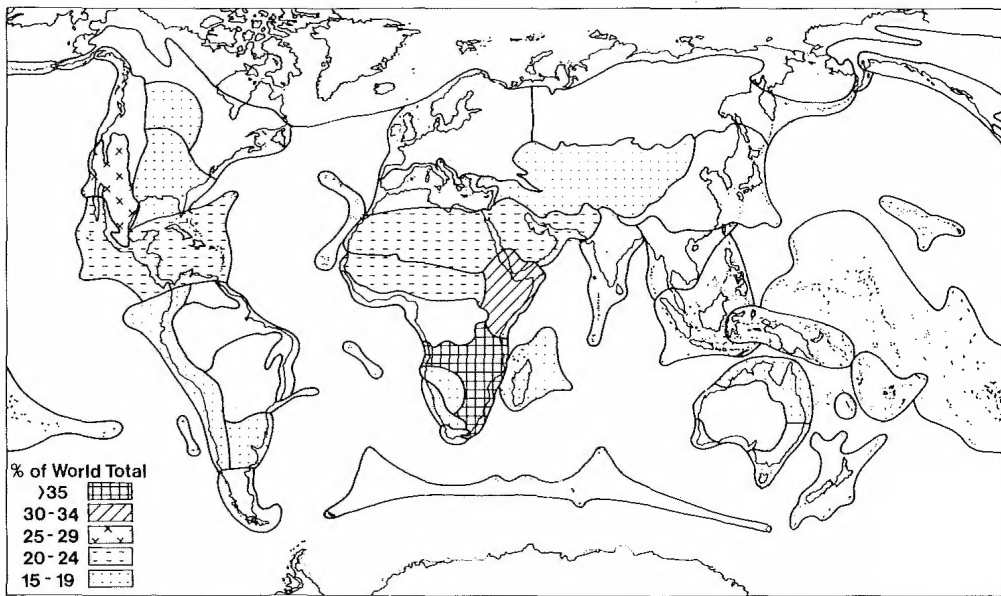
Map 3. Distribution of chloridoid genera.
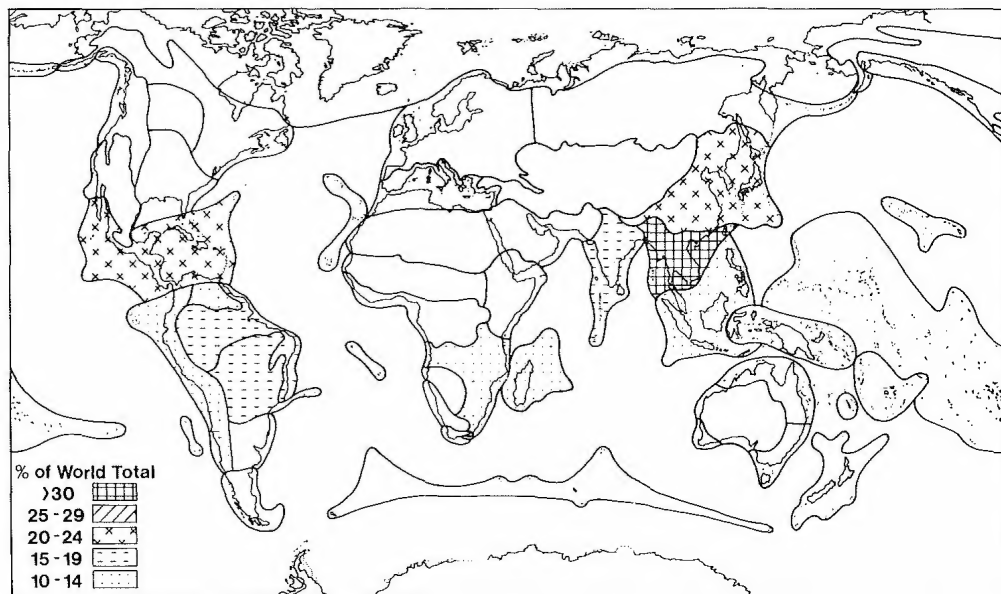
Map 4. Distribution of bambusoid genera.

form a large component of the grass flora in high altitude areas (and areas of high latitude in Australia and generally)."

Her statement that the "Bambusoideae has very few taxa and never forms a major component of the grass flora" is applicable to the situation in Australia but not generally. Although the distribution of grasses in Australia has been correlated by Hattersley (1983) with the photosynthetic pathway the results have not been extended to subfamily regions in the way that Gibbs-Russell has done for southern Africa, although an attempt has been made to correlate the decarboxylation types of C_4 grasses to geographical regions (Prendergast *et al.* 1986, Prendergast 1989).

Due to the active role Australia has had in the development of introduced pastures there is a considerable grass flora of a much more recent exotic origin, both from tropical and temperate regions (Clifford & Simon 1981). Large areas of the Australian landscape are now dominated by exotic species and areas of the coastal tropics have been said to have been Africanised (Simon 1983) in the same way as the New World tropical grasslands (Parsons 1970). It was mainly in the the savannas of Africa that today's successful forage grasses co-evolved with a host of wild herbivores (Clayton 1983) although the same process was also occurring in other localities (Stebbins 1981).

Conclusion

After an examination of each of the seven major groups of grasses recognized by us (andropogonoids, panicoids, chloridoids, arundinoids, bambusoids, stipoids and pooids) with respect to their possible areas and methods of origin, we observe that all except the pooids are considered to be Gondwanan in origin. This conclusion is in basic agreement with that of Clifford and Simon (1981). However none of these groups, on the basis of the accounts given in this paper, can be considered to be authochthonous in the sense of some rainforest groups (Webb, Tracey & Jessup 1986), in that they, or their precursors, all originated in other areas of Gondwanaland and made their way here subsequently. After arrival, adaptation to aridity and to extremes of soil types in the Tertiary (Specht 1981) became the main challenge faced by all plant groups and in the grasses a number of strategies must have been used by the genera *Aristida, Enneapogon, Eragrostis* and *Triodia*, that now dominate the arid zones of the continent (Jacobs 1982).

Acknowledgements

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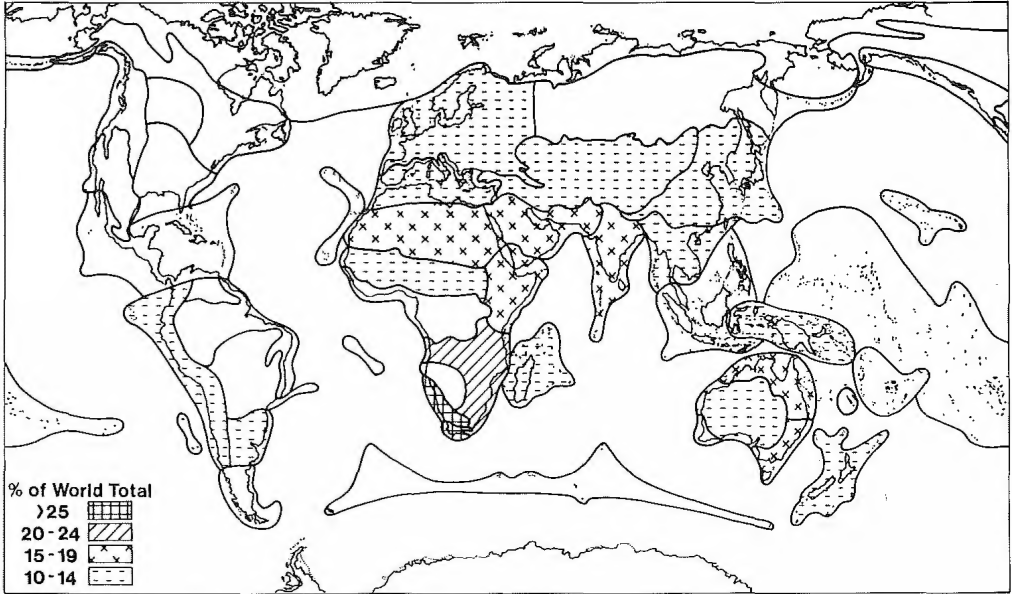
Map 5. Distribution of arundinoid genera.
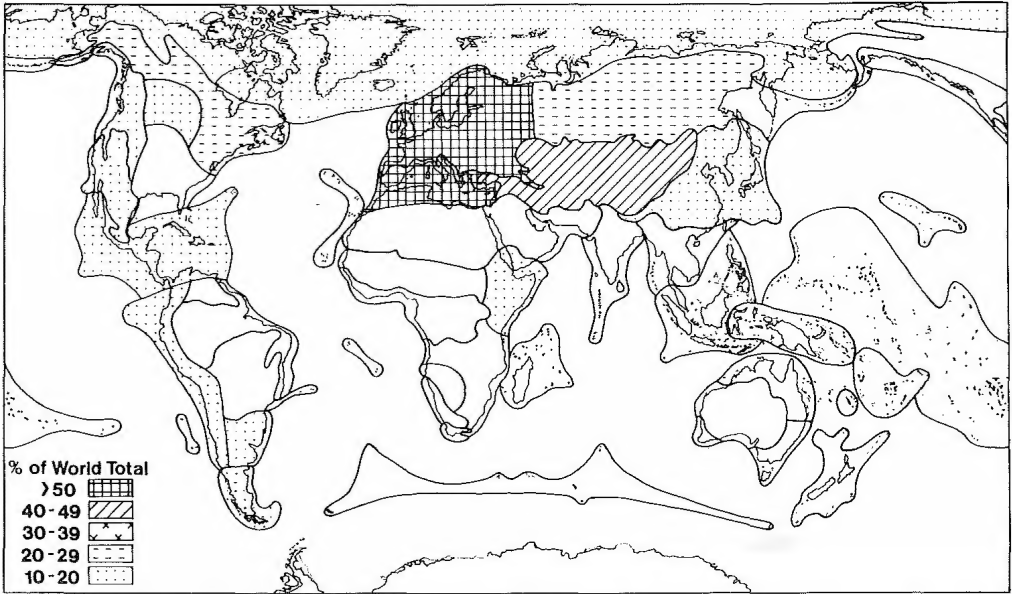
Map 6. Distribution of pooid genera.

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